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Observations on the benthic marine algal flora of South Georgia: a floristic and ecological analysis

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CONTENTS

Synopsis. The pattern of littoral zonation of benthic algae on rocky and boulder shores in Husvik Harbour, on the north-east coast of South Georgia, was investigated during the austral summer of 1990/91. Distribution patterns are similar to those on other shores in the sub-Antarctic region of the Southern Ocean, except for the absence in the littoral fringe of a '*Hildenbrandia*' or '*Hildenbrandia-Bostrychia* association'. The supralittoral fringe is devoid of macroalgae and gives way to a eulittoral zone consisting of a series of belts. An uppermost belt dominated by *Porphyra* followed by ones dominated or co-dominated by *Nothogenia fastigiata*, *Iridaea cordata*, and *Adenocystis utricularia*. The lowermost belt is either dominated by *Palmaria georgica* or co-dominated by this red alga and *Schizoseris condensata*. The upper vertical limit of crustose coralline algae and the kelps *Macrocystis pyrifera* and *Durvillaea antarctica* define the sublittoral fringe; the latter is only present on wave-exposed shores. The 103 species of algae known from South Georgia are critically evaluated, four are endemics and 12 are known only from South Georgia and Tierra del Fuego. The biogeographical affinities of the algal flora of South Georgia lies with other sub-Antarctic islands and the southern tip of mainland America.

INTRODUCTION

South Georgia is an isolated island in the Southern Ocean that lies between latitudes 53°56′–54°55′S and longitudes 34°45′–38°15′W. It is roughly crescent-shaped (Fig. 1) and the second largest of the circum-Antarctic islands. Its steep rocky coast, dissected by deep fjords and bays, provides suitable though very hostile habitats for benthic organisms. The algal flora of South Georgia remains little-known since biological exploration has been limited to a few bays on the more sheltered north-east coast. The first publications specifically on its marine algae are those of Reinsch (1888, 1890) and were based on material collected by the 1882–1883 German International Polar Year Expedition. The next major period of collecting on the island was during the 1901–1903 Swedish South Polar Expedition, but most of the material was lost when the expedition's ship 'Antarctica' foundered. Fortunately, the journals belonging to the expedition's botanist, Carl Skottsberg, survived and he re-visited the island in 1909 to make further observations and new collections. Information contained in his journals was used to write an ecological account of South Georgian algae which was subsequently published (Skottsberg, 1941). Some of the numerous expeditions en route to higher Antarctic latitudes have found safe anchorage at South Georgia and used the opportunity to collect algae from its shores.

Accounts of the ecology of Antarctic and sub-Antarctic marine algae still remain almost wholly descriptive. Early information on sublittoral assemblages was obtained indirectly by trawling, dredging and the collection of drift plants. The advent of SCUBA diving has enabled direct observations and the hand collection of undamaged specimens of sublittoral algae at several localities in the Southern Ocean (Neuschul, 1968; Délepine et al., 1966; Lamb & Zimmermann, 1977). Unfortunately SCUBA diving to investigate algal ecology has yet to be carried out on South Georgia. Observations on its sublittoral algal ecology date back to the early years of this century and are restricted to dredged collections (see Skottsberg, 1941). Although incomplete and unevenly distributed, there is sufficient information to enable some preliminary conclusions to be reached on the distribution patterns of littoral algae in the Southern Ocean (see Stephenson & Stephenson, 1972; Luning, 1990; Délepine et al., 1966; Zaneveld, 1964). Few experimental studies and the absence of reliable quantitative data have meant that information is lacking on ecological interactions involving algae.

The present study examines the distribution and abundance of shore algae on the north-east coast of South Georgia, critically reviewing all published and unpublished records, and makes some observations on the biogeographical affinities of its algal flora.

MATERIALS AND METHODS

Five transects were studied at Husvik Harbour (36°40′W, 54°11′S), Stromness Bay on the north-east coast of South Georgia (Fig. 1). This relatively wave-sheltered bay has small rocky outcrops of volcanoclastic sandstone-shale turbidite (Macdonald et al., 1987) separated by coarse sand or gravel beaches; all its shores are free from ice-scouring. Three of the transects were on rocky shores: A was north of the whaling station and below the catcher boat ‘Karrakatta’ on its repair slipway; B and C were on the southern side of the Harbour and on the west (B) and east side (C) of Kanin Point (Fig. 1). The other two transects were on boulder shores at Brain Island Point (D) on the northern side of Husvik Harbour and between the Husvik ‘villa’ and Kanin Point (E) on the southern shore.

The benthic algal communities on shores in Husvik Harbour were monitored at intervals from October 1990 to mid-January 1991. It was considered that by the end of the period the cover abundance of shore algae was close to its seasonal maximum. The distribution and cover of macroalgae were determined between 25 January and 15 February 1991 along the five shore transects. Each transect was surveyed from low water to the top of the supralittoral fringe using an Abney level mounted on a wooden block to give a base to horizontal line-of-sight distances of 20 cm. Slope distance between stations along a transect was measured with a tape. From these data both horizontal and vertical distances between sampling stations were calculated and shore profiles drawn (see Fig. 2). Vertical heights were corrected to Chart Datum (C.D.) using Admiralty Tide Tables (Admiralty, 1990, 1991). The tidal range is *c.* 1.2 m and the cumulative measurement error was +0.1 m at high water mark.

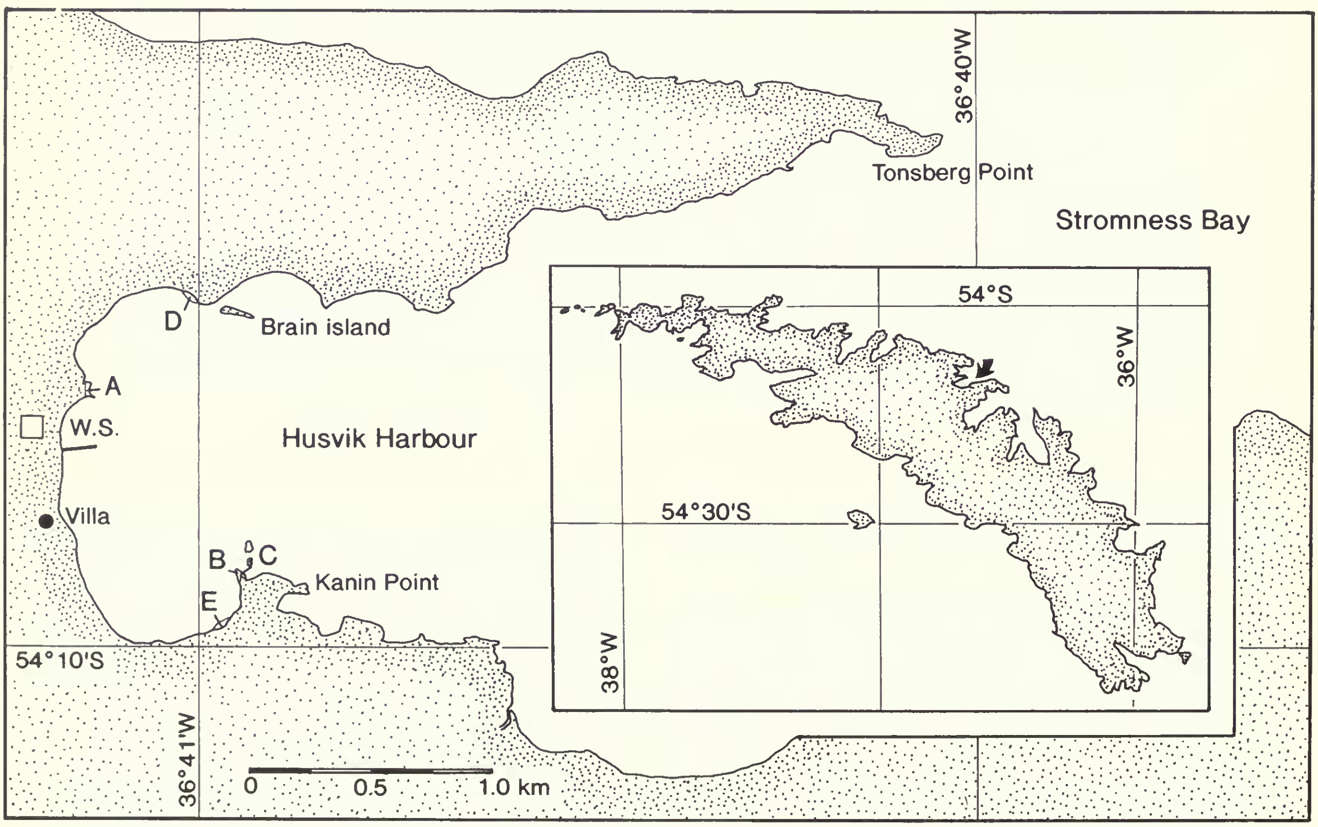

Fig. 1 Map of Husvik Harbour on the north-east coast of South Georgia showing the position of the five investigated transects (A–E). Insert of South Georgia shows an arrow indicating the position of Husvik Harbour. W.S., whaling station.

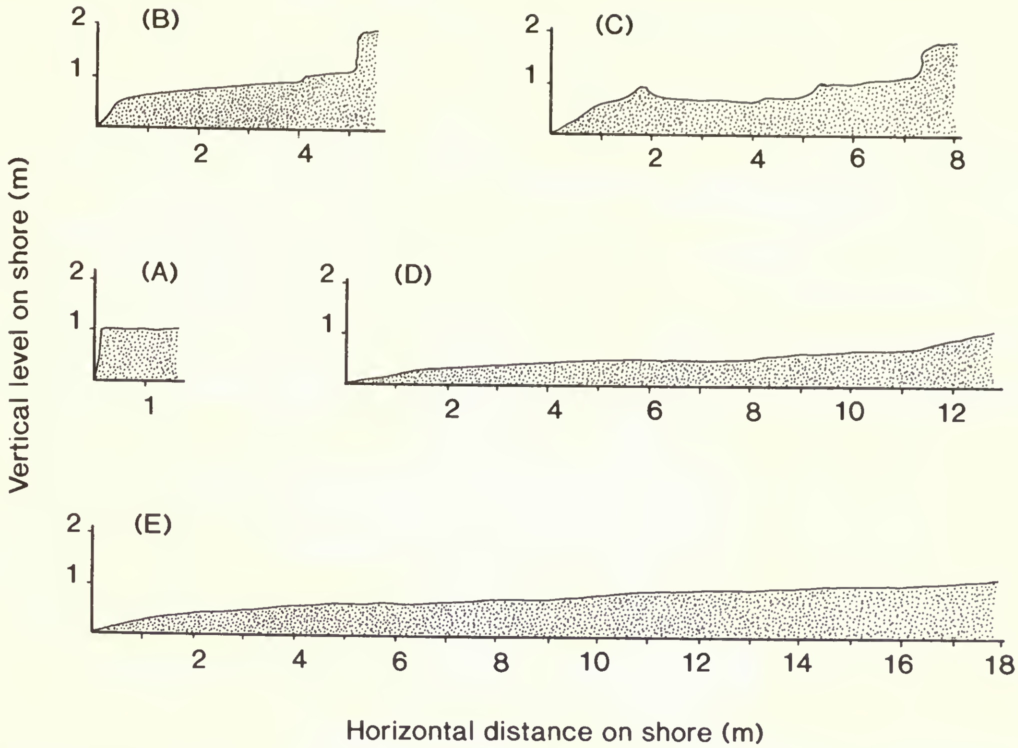

Fig. 2 Shore profiles of the five transects.

The algal assemblages were photographed in situ and all material collected was preserved in 5% seawater-formalin. The relative cover abundance of the dominant macroalgae at each sample station was calculated to within ±3% and expressed as a percentage of total rock covered. All algal specimens are deposited in the Herbarium at The Natural History Museum, London.

RESULTS

Distribution of shore algae

Despite the small tidal amplitude (*c.* 1.2 m) marine influences extend vertically by several metres where the coast is exposed to heavy swells and severe wave action. Only in rocky bays and inlets is the sea sufficiently calm to enable a detailed analysis of the distribution of shore organisms. In Husvik Harbour, the upper limit of the littoral zone is about 1.5–1.7 m above C.D. on rocky shores (Figs 3–5) and 0.75–1.2 m on the boulder shores (Figs 6–7), based on the vertical limit of the membranaceous red alga *Porphyra*. Total algal cover shows considerable variation (Fig. 8) in response to several factors well-known to influence algal abundance and distribution, i.e. shore topography (see Fig. 2), shore aspect, nature of the substratum, and type and degree of exposure to water motion. Rocky shore transect A is partially shaded, faces due south and is positioned along a surge channel. Transects B and C run across rocky shores that are in close proximity to each other (see Fig. 1), the former more wave-sheltered due to the presence of a rock spur. The other two transects (D, E) run over gently sloping boulder shores and most algae are restricted to the sides of the boulders. *Porphyra* accounts for the high total algal cover on the upper part of the eulittoral zone in transects B and E.

The algal vegetation of the rocky shores (Figs 3–5) comprises 12 to 13 species. The upper eulittoral was dominated by *Porphyra* whose cover-abundance was particularly high on gently sloping shores (B, C; see Fig. 2). Associated with *Porphyra* were *Nothogenia fastigiata* and *Iridaea cordata*; these latter two red algae were found commonly in protected niches. They were not present higher than 1.1 m above C.D. and tended to be confined to the lower part of the *Porphyra* belt. The lower eulittoral zone was dominated by the red alga *Palmaria georgica*, accompanied by lesser amounts of *Porphyra* sp., *Schizoseris condensata* and *Adenocystis utricularis*; the latter grew as isolated clumps or single plants confined to sheltered niches. In the lower eulittoral zone the filamentous red alga *Ceramium rubrum* was frequently intermingled with clumps of *Schizoseris*. Small *Macrocystis* and encrusting calcareous red algae ('lithothamnia') were observed around Chart Datum and below.

Only 7–9 algal species were found on the boulder shores D and E (Figs 6, 7), with the former unusual in having a sparse cover of *Porphyra* and a lower eulittoral zone dominated by colonial diatoms. The brownish layer of diatoms covered the sides of many boulders, occupying the position of the *Palmaria*/*Schizoseris* association on rocky shores. The upper eulittoral of shore E was dominated by *Porphyra*, confined to the sides of boulders, and the lower eulittoral zone had a very sparse covering of a mixture of algae.

Systematic list

A list of the marine benthic algae from South Georgia based on a critical evaluation of published records, and an examination of material collected by one of us (PJAP) in January and

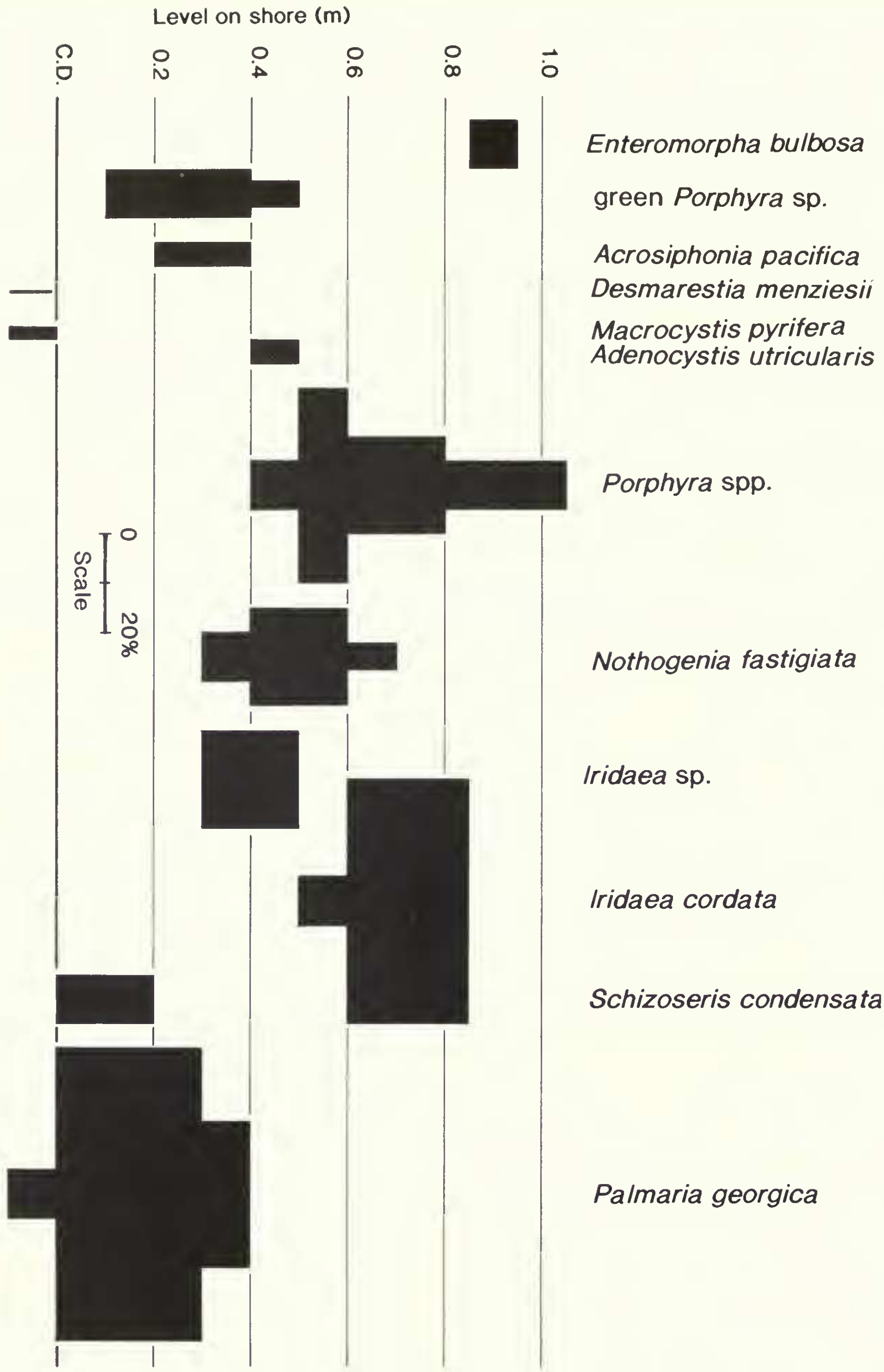

Fig. 3 The vertical distribution and percentage cover abundance of seaweeds on the rocky shore transect A.

February 1991 and specimens in the Herbarium of The Natural History Museum, London. Nomenclatural revisions and re-examination of material has resulted in some of the species listed here published under different names. Given under each entry is the name(s) by which the species has been reported in the list area (synonyms, misdeterminations). For further information on many of the entries, see Papenfuss (1964). Qualifying notes accompany some of the entries especially where there is an element of doubt attached to the records.

Chlorophyta

Acrosiphonia pacifica (Montagne) J. Agardh
Reported as *Cladophora arcta*, *C. pacifica*, *Spongomorpha arcta* and *S. pacifica*.
Cladophora incompta (Hooker f. & Harvey) Hooker f. & Harvey

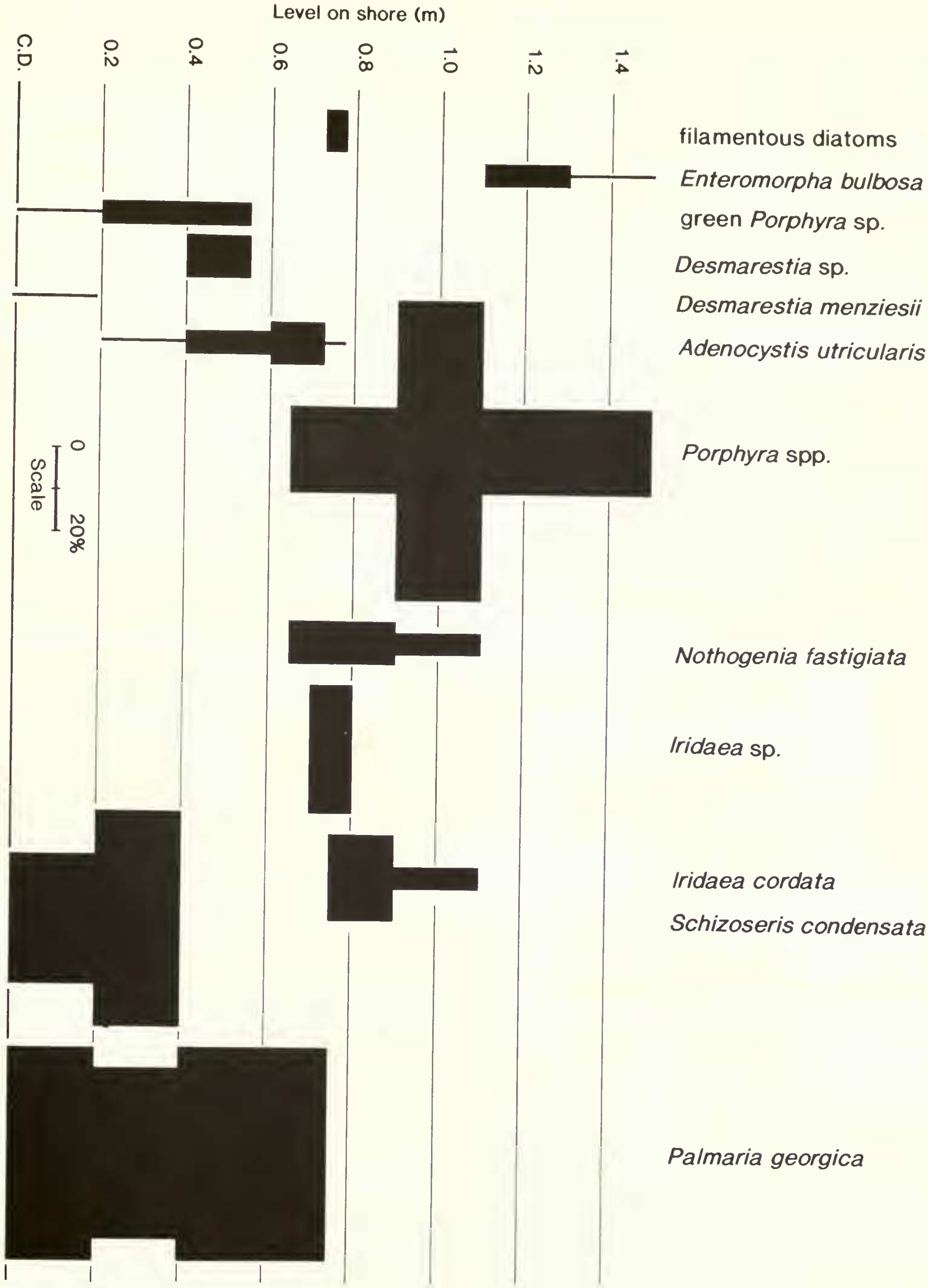

Fig. 4 The vertical distribution and percentage cover abundance of seaweeds on the rocky shore transect B.

Enteromorpha bulbosa (Suhr) Montagne
Reported as *E. novae-hollandiae*.
All plants collected during the Swedish 1907–1909 expedition and attributed to this species by Hylmo (1919) may equally well be a form of *E. intestinalis* (see Ricker, 1987: 36). The principal features distinguishing *E. bulbosa* from *E. intestinalis* are the smaller dimensions of its cells and their thicker walls (Lamb & Zimmermann, 1977), or the absence of any branching of the thallus (Ricker, 1987).

Enteromorpha gunniana J. Agardh
Closely related to *E. bulbosa*, with a plant from Macquarie Island attributed to *E. gunniana* by Ricker (1987: 36) considered to fall

Fig. 5 The vertical distribution and percentage cover abundance of seaweeds on the rocky shore transect C.

within the form range of *E. bulbosa*. Doubt attaches to the species identification of this alga from South Georgia.

Entonema subcorticale Reinsch
This taxon and the following are little-known epiphytes, possibly identical to *Entocladia* (see Ricker, 1987: 24).

Entonema tenuissimum Reinsch

?Prasiola crispa (Lightfoot) Meneghini subsp. **antarctica** (Kuetzing) Knebel
Recorded as *P. antarctica*.
Doubtful record as no text entry and yet listed in Reinsch's index (Reinsch, 1890); this is the likely source of Hylmo's (1919) secondary citation.

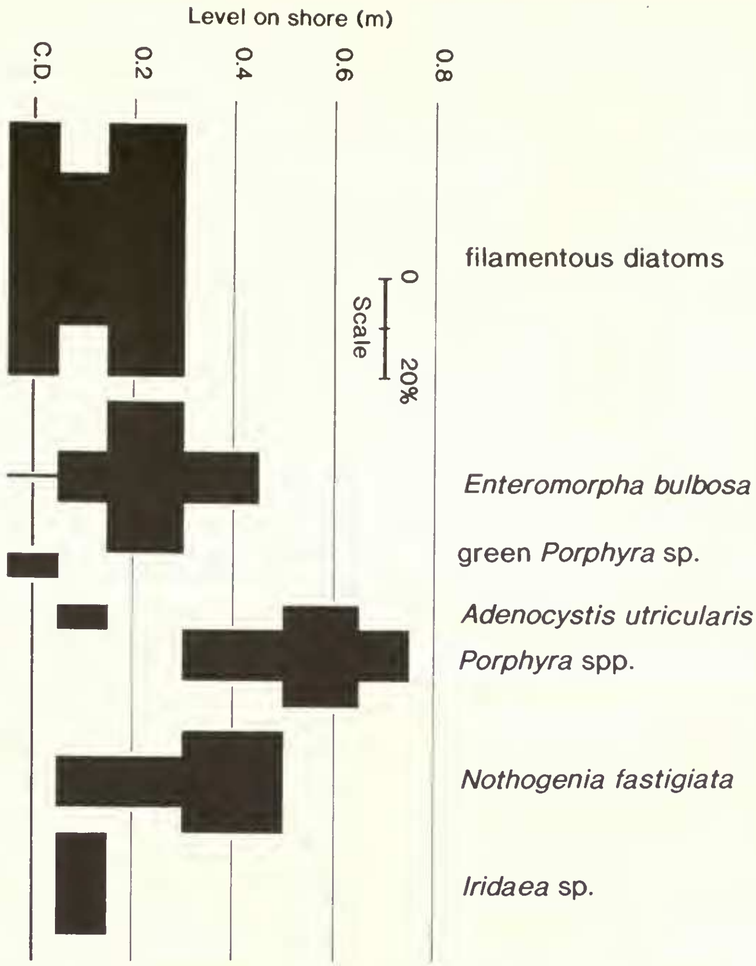

Fig. 6 The vertical distribution and percentage cover abundance of seaweeds on the boulder shore transect D.

Prasiola filiformis Reinsch var. **minuta** Reinsch
Status of this taxon requires investigation.

Ulothrix sp.
Reported as *Hormiscia parasitica*.
According to Papenfuss (1964: 1), this record is 'probably representative of one of the species of *Ulothrix* that has been reported from Antarctica'.

Ulva lactuca Linnaeus var. **macrogyna** Reinsch
Status of this taxon requires investigation.

Phaeophyta

Adenocystis utricularis (Bory de Saint-Vincent) Skottsberg
Recorded as *Chroa sacculiformis*.

Ascoseira mirabilis Skottsberg
Reported as *Lessonia fuscescens* var. *linearis*.

Caepidium antarcticum J. Agardh

Cladothele decaisnei Hooker f. & Harvey
Recorded as *Stictyosiphon decaisnei*.

Corycus lanceolatus (Kuetzing) Skottsberg
Recorded as *C. prolifer*.

Desmarestia antarctica Moe & Silva
South Georgia is its northernmost limit of distribution. Its minute gametophytic stage is endophytic on *Curdiae recovitzae* (see Moe & Silva, 1989), a red alga also at the limit of its range.

Desmarestia ligulata (Lightfoot) Lamouroux
Recorded as *D. firma*.

Desmarestia menziesii J. Agardh
Recorded as *D. aculeata* var. *compressa*, *D. compressa* and *D. harveyana*.

Desmarestia pteridoides Reinsch
Status of this plant remains uncertain, see remarks in Skottsberg (1907: 20).

Desmarestia willii Reinsch
This southern hemisphere species is closely related to *D. viridis* known only from the northern hemisphere. According to Ricker (1987: 126), the southern hemisphere species shows wide variation in key characters and so is less distinct than Reinsch (1888: 191) indicated when justifying its creation.

Durvillaea antarctica (Chamisso) Hariot

Ectocarpus constanciae Hariot
Ricker (1987: 67) separates it from *E. siliculosus* upon its greater cell diameters, tapering of apical branches, absence of hook-shaped laterals, presence of fewer corticating rhizoids covering lower axes, helical coiling of ribbon-like plastids, and more elongate and solitary plurangia. He accepts that the two species may form part of the form range continuum of *E. siliculosus*.

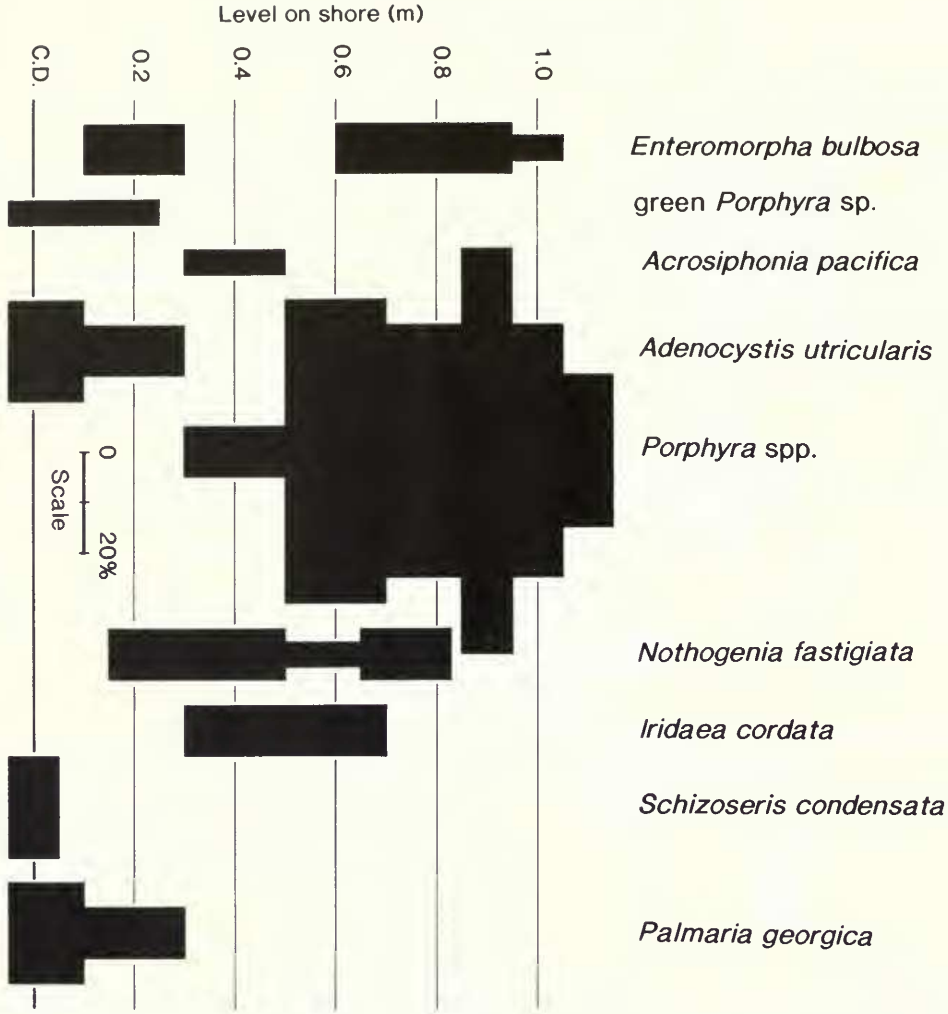

Fig. 7 The vertical distribution and percentage cover abundance of seaweeds on the boulder shore transect E.

Ectocarpus exiguus Skottsberg
Recorded as *E. humilis*.

Ectocarpus siliculosus (Dillwyn) Lyngbye
Recorded as *E. confervoides* and *E. fasiculatus*.

Elachista meridionalis Skottsberg

Geminocarpus austrogeorgiae Skottsberg

Geminocarpus geminatus (Hooker f. & Harvey) Skottsberg
Recorded as *Ectocarpus geminatus*.

Halopteris funicularis (Montagne) Sauvageau
Recorded in table (Skottsberg, 1941: 76) showing Antarctic distribution of algae. No indication given as to source and not mentioned in Papenfuss's (1964) catalogue of Antarctic and sub-Antarctic algae.

Halopteris obovata (Hooker f. & Harvey) Sauvageau

Himantothallus grandifolius (A. & E.S. Gepp) Zinova
Recorded as *Laminaria saccharina* var. *angustata*, *Himantothallus spiralis* and *Phyllogigas grandifolius*.

Lessonia fuscescens Bory
Recorded as *L. flavicans*.
It seems very likely that this large brown alga, characteristic of many sub-Antarctic shores, grows attached on South Georgia despite Skottsberg's (1921) statement (p. 47) that 'Drifted pieces have been observed along the coast of S. Georgia where according to my impression this plant does not grow'.

Macrocystis pyrifera (Linnaeus) C. Agardh
Recorded as *M. pyrifera* var. *longibullata*.

Melastictis desmarestiae Reinsch
Status of this monotypic genus is uncertain.

Myrionema densum Skottsberg

Myrionema incommodum Skottsberg
Adenocystis the host alga.

Myrionema inconspicuum Reinsch
Very similar to *M. densum* and *M. corunnae*; Skottsberg (1921) suggests *M. inconspicuum* and *M. densum* to be conspecific.

Myrionema macrocarpum Skottsberg
Record from a table showing Antarctic distribution of algae (Skottsberg, 1907). No indication given as to source and Papenfuss (1964) does not mention it from South Georgia.

Myrionema? paradoxum Reinsch
Reinsch's description and illustration of this species and *M. inconspicuum* (Reinsch, 1890) are equivocal, see comments in Ricker (1987: 83).

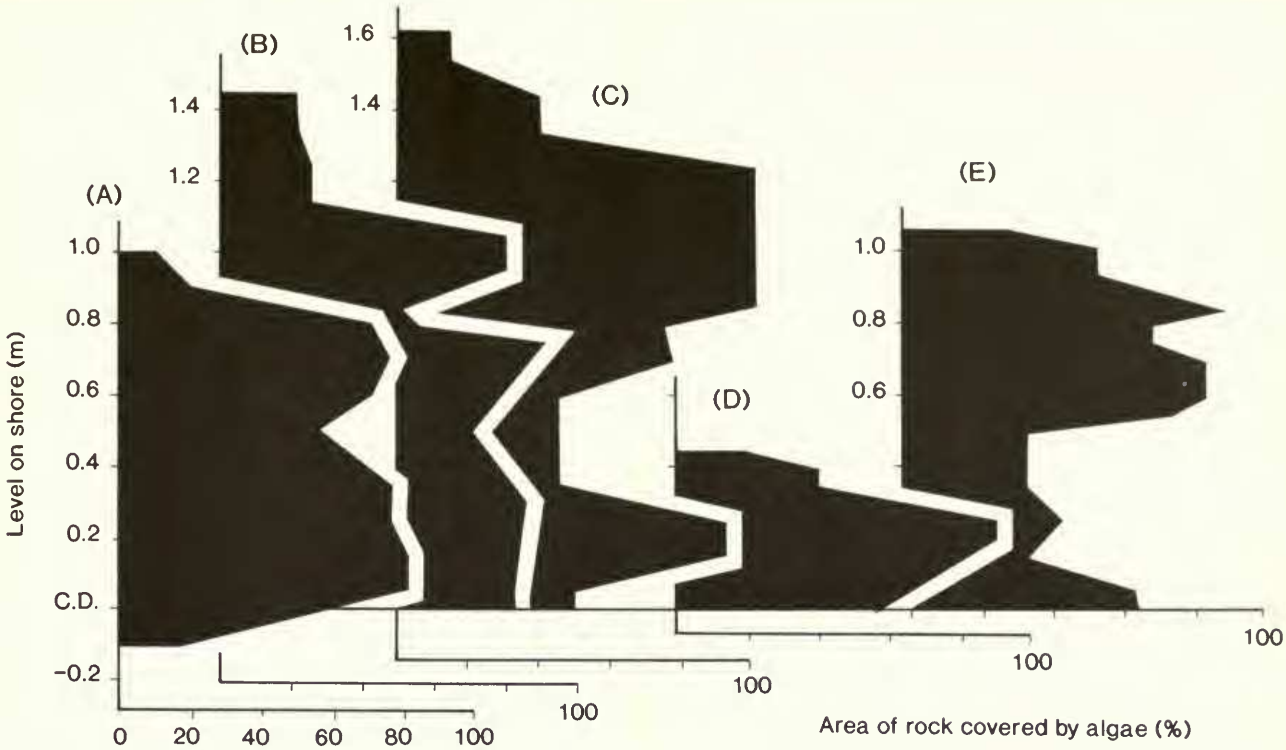

Fig. 8 Total percentage cover abundance of seaweeds at different levels on each of the five shore transects.

Petalonia fascia (O.F. Mueller) Kuntze
Recorded as *Phyllitis fascia* and *Ilea fascia*.

Petroderma maculiforme (Wollny) Kuckuck

Phaearthron austrogeorgica (Skottsberg) Pedersen
Recorded as *Xanthosiphonia austrogeorgica*.

Pilayella littoralis (Linnaeus) Kjellman
Recorded as *Pylaiella opposita*.

Scytosiphon lomentaria (Lyngbye) Link

Scytothamnus fasciculatus (Hooker f. & Harvey) Cotton
Recorded as *S. australis*.

Stegastrum porphyrae Reinsch
Status of this monotypic genus is uncertain.

Syringoderma australe Levring

Utriculidium durvillaei (Bory) Skottsberg
Morphologically very similar to *Adenocystis utricularis*. Differs in the cortical cells possessing a single (not several) plastid and only plurilocular sporangia known. Some authors have suggested that they are alternate phases of a single species.

Rhodophyta

Ahnfeltia plicata (Hudson) Fries

Anisocladella serratodentata (Skottsberg) Skottsberg
Recorded as *Delesseria erratodentata*.

Antithamnion ptilota (Hooker f. & Harvey) Gibson
Ricker (1987: 240) examined the type (*Callithamnion ptilota* Hooker f. & Harvey, 1845) and concluded that it 'may be identical to *D*[*asyptilon*]. *pellucidum*, as both species have similar apical development and branching patterns'. He left unresolved the question of conspecificity since no reproductive structures were present on the type. If they should prove to be conspecific then the correct epithet for the species will be *Dasyptilon ptilota*.

Ballia callitricha (C. Agardh) Kuetzing

Bostrychia vaga Hooker f. & Harvey

?Calliblepharis ciliata (Hudson) Kuetzing
Recorded as *Rhodymenia ciliata* var. *ligulata*.
The identity of this plant remains uncertain.

Callithamnion montagnei Hooker
A new record for South Georgia and deposited in the Herbarium in the Department of Botany, The Natural History Museum, London. It was discovered as one of three red algae (*Ceramium rubrum*, *Plocamium secundatum*) entangled with or growing epiphytically on a specimen of *Phycodrys quercifolia* collected from Possession Bay in January 1867 by Dr R.O. Cunningham.

?Callonema olivaceum Reinsch
The identity of this taxon remains uncertain (Papenfuss, 1964).

?Callophyllis cristata (C. Agardh) Kuetzing
Recorded as *Euthora cristata* and *Rhodymenia cristata*.
A questionable determination according to Skottsberg (1941).

Callophyllis linguata Kylin

Callophyllis variegata (Bory de Saint Vincent) Kuetzing
Recorded as *Kallymenia multifida* and *Callymenia multifida*.

Ceramium diaphanum (Lightfoot) Roth

Ceramium involutum Kuetzing

Ceramium rubrum (Hudson) C. Agardh

?Choreocolax rhodymeniae Reinsch
Parasitic alga on *Palmaria*.
The identity of this species remains uncertain.

Cladodonta lyallii (Hooker f. & Harvey) Skottsberg
A new record for South Georgia based on three specimens in the Herbarium in the Department of Botany, The Natural History Museum, London. Material collected in January 1867 by Dr R.O. Cunningham from Possession Bay during the extra-tropical South America survey of H.M.S. Nassau.

Clathromorphum obtectulum (Foslie) Adey
Recorded as *Lithophyllum aequabile*, *L. discoideum* f. *aequabilis* and *Antarcticophyllum aequabile*.

Colacodasya inconspicua (Reinsch) Schmitz
Recorded as *Polysiphonia inconspicua* and *Merenia inconspicua*. Parasitic on *Heterosiphonia*.

Curdiea recovitzae Hariot ex Wildemann
Recorded as *Kallymenia reniformis* f. *carnosa* and *Callymenia reniformis*.

Delesseria salicifolia Reinsch
Indistinguishable on vegetative features from *D. lancifolia*, but separated on form of the cystocarp and specialized sporophylls containing tetrasporangia.

Delisea pulchra (Greville) Montagne
Recorded as *Bonnemaisonia prolifera*.

Falklandiella harveyi (Hooker f.) Kylin
Recorded as *Dasyptylon harveyi*, *Plumaria harveyi* and *Euptilota harveyi*.
For discussion of distinctions between this genus and others including *Dasyptilon*, see Moe & Silva (1979).

Georgiella confluens (Reinsch) Kylin
Recorded as *Ptilota confluens*, *Euptilota confluens* and *Plumariopsis eatoni*.
This genus and *Plumariopsis* are endemic to the southern hemisphere and are morphologically similar. Moe & Silva (1983) tabulate a number of vegetative and reproductive features that distinguish them.

Heterosiphonia berkeleyi Montagne
Recorded as *Merenia microcladioides* and *Heterosiphonia merenia*.

Hydrolithon discoideum (Foslie) Mendozoa & Cabioch
Recorded as *Lithophyllum discoideum*, *Pseudolithophyllum discoideum* and *Spongites discoidea*.

?Hymenocladiopsis crustigena Moe
Recorded as *Gracilaria prolifera*.
Doubt concerns the exact status of the South Georgian material. Moe (1986) has investigated the type of *Gracilaria prolifera* and states that it is 'certainly placed incorrectly as to genus .. Although nothing precludes its assignment to *Hymenocladiopsis*, I hesitate to propose a new combination without seeing tetrasporangial material or material in which the presence or absence of gland cells can be determined with certainty. It is possible that the plants from the Antarctic Peninsula on which the new genera is based are conspecific with *Gracilaria prolifera*'. Should this prove to be the case then the epithet '*prolifera*' would have priority.

Iridaea cordata (Turner) Bory de Saint-Vincent
Recorded as *I. micans* and *I. cordata* f. *ligulata* (type locality of trivial growth form).
Leister (1977) regards several earlier described species as conspecific with *I. cordata*.

Iridaea obovata Kuetzing
Recorded as *Iridaea macrodonta* and *Rhodoglossum macrodontum*.

Microrhinus carnosus (Reinsch) Skottsberg
Recorded as *Delesseria carnosa* and *Chauvinia carnosa*.

Mesophyllum schmitzii (Hariot) Mendoza
Recorded as *Lithothamnion schmitzii*.
The original record on which this report is based has not been traced (see Ricker, 1987: 175).

?Myriogramme livida (Hooker f. & Harvey) Kylin
Skottsberg (1941: 76) tabulated the distribution of Antarctic and sub-Antarctic algae. No indication was given as to source and Skottsberg's record was not mentioned by Papenfuss (1964) in his catalogue of Antarctic and sub-Antarctic algae.

Myriogramme smithii (Hooker f. & Harvey) Kylin
Recorded as *Nitophyllum fuscorubrum* and *N. smithii*.

Nereoginkgo adiantifolia Kylin

Neuroglossum ligulatum (Reinsch) Skottsberg
Recorded as *Delesseria ligulata* and *Choreocolax delesseriae*.

Nothogenia fastigiata (Bory de Saint-Vincent) Parkinson
Recorded as *Chondrus crispus* var. *pigmaeus* and *Chaetangium fastigiatum*.

Palmaria decipiens (Reinsch) R.W. Ricker
Recorded as *Rhodymenia decipiens, R. palmata* sensu Reinsch, *R. palmetta* var. *multiloba*, *Leptosarca alcicornis* and *L. decipiens*.
According to Ricker (1987: 221), it is morphologically very similar to the type species of *Palmaria* (*P. palmata*) but distinguished by the readiness of its tissues to soften in 4% formalin-seawater.

Palmaria georgica (Reinsch) R.W. Ricker
Recorded as *Rhodymenia georgica*, *R. palmatiformis* and *R. palmatiformis* var. *austrogeorgica*.
The overlap in thallus morphology of the two *Palmaria* species has led Ricker (1987: 224) to suggest that *P. georgica* may be 'merely a diminutive form or an ecotype of *P. decipiens*'. *P. georgica* separates from *P. decipiens* by forming tufts composed of many fronds, its bushier form, presence of cortical hairs, and occupying a different habitat.

Pantoneura plocamioides Kylin

Phycodrys austrogeorgica Skottsberg

Phycodrys quercifolia (Bory) Skottsberg
Recorded as *Delesseria quercifolia*.

Phyllophora antarctica A. & E.S. Gepp
Recorded as *Ahnfeltia plicata* and *Phyllophora ahnfeltioides*.

Phyllophora appendiculata Skottsberg
According to Skottsberg (1953: 542), this species might be identical with *Gymnogongus turqueti* Hariot (a *Phyllophora*, see Ricker, 1987: 202).

Picconiella plumosa (Kylin) De Toni
Recorded as *Dasya? pectinata* and *Pteronia plumosa*.

?Plectoderma minus Reinsch
Uncertainty surrounds the taxonomic status of this taxon. The genus was established by Reinsch (1874) for two species of simple, crustose coralline algae. According to Chamberlain (1983: 308), this species 'was probably *Melobesia membranacea* judging by the cell shape and general disc pattern . . . No specimens have been found of either species so further identification is not possible'.

Plocamium cartilagineum (Linnaeus) Dixon
Recorded as *P. coccineum*.

Plocamium hookeri Harvey

Plocamium secundatum (Kuetzing) Kuetzing

Polycoryne radiata Skottsberg
Parasitic on *Schizoseris dichotoma*.

Polysiphonia anisogona Hooker f. & Harvey

Porphyra endiviifolium (A. & E.S. Gepp) Chamberlain
Recorded as *Monostroma endiviifolium*.
Chamberlain (1963: 152) believed Hylmo's (1919: 6) record from South Georgia was based on a misidentification. New collections from the island now confirm its presence.

Porphyra umbilicalis (Linnaeus) Kuetzing
Recorded as *P. laciniata* and *Wildemannia laciniata*.

Pseudolaingia larsenii (Skottsberg) Levring
Recorded as *Delesseria larsenii*.

Pterothamnion simile (Hooker f. & Harvey) Naegeli
Recorded as *Callithamnion pinastroides* var. *ramulosum*, *Antithamnion ramulosum* and *A. simile*.

Sarcodia montagneana (Hooker f. & Harvey) J. Agardh

Schizoseris condensata (Reinsch) R.W. Ricker
Recorded as *Delesseria condensata*, *Nitophyllum condensata*, *N. multinerve* pro parte, *N. affine*, *Schizoseris laciniata* and *Delesseria laciniata*.
See Ricker (1987: 285, 286) for discussion of nomenclature and synonymy.

Schizoseris dichotoma (Hooker f. & Harvey) Kylin
Recorded as *Delesseria polydactyla*, *Myriogramme multinervis*, *Nitophyllum polydactylum* and *Schizoseris polydactyla*.

Synarthrophyton patena (Hooker f. & Harvey) Townsend
Recorded as *Lithothamnium antarcticum*.

Rejected records

Cystosphaera jacquinotii (Montagne) Skottsberg
South Georgia: Neuschul (1968). Despite mentioning this taxon as occurring at this locality in the text (p. 10), it is not indicated on his distribution map nor the source of the record given (see Lamb & Zimmerman, 1977: 174).

Plumariopsis eatoni (Dickie) De Toni
The report of this taxon from South Georgia by Kylin & Skottsberg (1919) is probably a misdetermination for the closely related **Georgiella confluens** (see above). Moe & Silva (1983) believe this species does not occur in Antarctica despite earlier reports.

DISCUSSION

Shore ecology

The upper part of the eulittoral zone of rocky shores within Husvik Harbour is dominated by belts of *Porphyra* or mixed belts of *Porphyra*/*Nothogenia*. Similar belts were described by Skottsberg (1941) at this shore level at May Cove (=Maiviken), Cumberland Bay where an '*Adenocystis*-Chlorophyceae association' was observed on the lower shore. Skottsberg makes no reference to belts of *Schizoseris* or *Palmaria*, but simply mentions that these two red algae were largely confined to tide pools containing a reasonably diverse algal community. He reported a '*Rhodymenia* [=*Palmaria*]-*Lithophyllum* association' in rock-lined pools and a '*Rhodymenia* [=*Palmaria*] association' in stony pools, while brackish-water pools contained *Adenocystis*, *Scytosiphon*, and *Utriculidium*. In the present study green algae were frequent in the littoral zone although the two most abundant taxa (*Enteromorpha*, *Acrosiphonia*) did not form a distinctive belt. Only on boulder shores were green algae found to be relatively abundant. On one of the rocky shores a coating of a green filamentous alga was observed in the upper eulittoral zone (probably *Ulothrix*; not collected). No mention is made by Skottsberg (1941) of any green algae in his study of a stony beach at Boiler Bay (=Grytviken), Cumberland Bay where algal diversity was considerably less compared to the boulder shores studied at Husvik Harbour where *Adenocystis* and *Nothogenia* ('*Adenocystis-Chaetangium* [=*Nothogenia*] association') dominated. Unlike Husvik Harbour, the shores in Grytviken are affected by small icebergs ('growlers') produced by calving glaciers of which seven occur in the Cumberland Bay complex. Ice-scour and abrasion are known to be major physical factors affecting sessile shore organisms in high latitudes (see Keats et al., 1985).

Our observations on the distribution of shore algae show close agreement with many of those made by Skottsberg (1941) in the early years of this century. He was of the opinion that his general observations enabled him to have a 'fair idea of the composition of the vegetation [algae]' of South Georgia. Of the 21 stations described by Skottsberg, all were relatively sheltered and confined to north-easterly shores. If he had been as familiar with South Georgia as claimed then it is surprising that he overlooked the bull kelp *Durvillaea antarctica*, first reported by Will in 1890 and yet going unmentioned by Reinsch (1888, 1890) who determined his algal material. Will's report of *Durvillaea* growing on rocky headlands on South Georgia was confirmed by Hay (1988, based on personal observations by Knowles) who states it forms (p. 426) 'a distinctive band in the low intertidal zone on the outer coast between Cumberland Bay and Royal Bay'. In 1991 one of us (PJAP) found a large bed of *Durvillaea* growing in the sublittoral fringe at Tonsberg Point (see Fig. 1). A large proportion of the tidal drift within Husvik Harbour comprises *Durvillaea*, much of it probably originates from this Point. On wave-exposed coasts *Durvillaea antarctica* characterizes the sublittoral fringe as reported on other sub-Antarctic shores (see Stephenson & Stephenson, 1972).

The general distribution pattern of shore algae described on South Georgia during the short austral summer resembles those of sub-Antarctic and Antarctic rocky shores so far investigated (Knox, 1960; Kenny & Haysom, 1962; Price & Redfearn, 1968; Smith & Simpson, 1985; Delepine et al., 1966; Stephenson & Stephenson, 1972, among others). Absent from the littoral fringe are macroscopic growths of algae and the upper eulittoral subzone is defined by the genus *Porphyra*, below which appears *Nothogenia*. Simpson (1976) used the upper limit of *Porphyra* to define the upper limit of the eulittoral zone on Macquarie Island. Most algae on the lower shore seem confined to pools with the exception of *Adenocystis*, *Iridaea*, *Schizoseris* and *Palmaria*. As mentioned above, these algae are present in the lower eulittoral zone and are common at this level on other shores of the Southern Ocean (see Stephenson & Stephenson, 1972). Calcareous coralline algae or 'lithothamnia', often characteristic of the lower eulittoral subzone on lower latitude shores, form evident crusts in the sublittoral fringe on South Georgia. These crusts correspond to the '*Lithophyllum-Lithothamnion* association' of Antarctic shores, an association typically confined to rock pools and whose upper limit indicates the mean low tide level on sloping rocky shores (see Delepine et al., 1966). The presence of a '*Hildenbrandia*' or '*Hildenbrandia-Bostrychia* association' on several sub-Antarctic shores has not been observed on South Georgia.

The sublittoral fringe on South Georgia is defined by the upper distributional limit of two kelps: juveniles of *Macrocystis pyrifera* on sheltered to moderately wave-exposed shores, and mature plants of *Durvillaea antarctica* on wave-exposed headlands. These brown algae characterize this fringe on sub-Antarctic and cold temperate shores, both reaching the southernmost limit of their distribution in South Georgia and Tierra del Fuego. The presence of *Macrocystis* on South Georgia led Skottsberg (1941) to remark (p. 36) that 'from the very first the visitor gets the impression that, regarded from an algological viewpoint, South Georgia must be included in the Subantarctic zone'. This statement was made at a time when Skottsberg had rejected *Durvillaea antarctica* as indigenous to the island.

The high diversity and biomass of subtidal algal vegetation markedly contrasts with the low diversity and comparative barrenness of the littoral zone. On rocky bottoms the large kelps are the canopy dominants. In the entrance to sheltered inlets such as Grytviken (=Boiler Bay), a '*Macrocystis-Desmarestia-Pteronia-Plocamium* association' was reported by Skottsberg (1941) as growing on stones down to a depth of 25 m. He noted that some of the dominant lower littoral algae (e.g. *Palmaria* sp. [as *Rhodymenia palmatiformis*]) grew to a depth as great as 30 m and described a number of associations which, albeit sampled indirectly by trawling, seemed to vary according to depth and substratum type.

Marine algal flora

The South Georgian algal flora is surprisingly diverse (103 species, 75 genera) considering the few shores (mostly wave-sheltered) investigated on its north-eastern coast during just a few austral summers. Undoubtedly species records for the island would increase if wave-exposed shores were visited and more subtidal collecting was undertaken. Skottsberg (1964), in recalling his two summers on South Georgia, states (p. 149) 'my journal from 1902–03 contains rough drawings of unknown Rhodophyceae lost in the shipwreck and never collected a second time'.

Of the 103 species of marine algae known from South Georgia, nine are green algae, 35 brown algae, and two of the 47 red algae are unpublished records (*Cladodonta lyallii*, *Callithamnion montagnei*). The island is the type locality for 32 species (four genera), and yet South Georgia has just four endemic species and one endemic genus (Tables 1, 2). The taxonomic status of these endemics and endemic infraspecific taxa (*Iridaea cordata* f. *ligulata*, *Prasiola filiformis* var. *minuta*, *Ulva lactuca* var. *macrogyna*) is questionable. Twelve algal species are known only from South Georgia and Tierra del Fuego (Kuhnemann, 1972), an island lying about 2150 km due west of it. About 22% of the South Georgian algae also occur in the Northern Hemisphere, while *Entonema tenuissimum*, *Calliblepharis ciliata*, *Callonema olivaceum* and *Callophyllis cristata* are only known in the Southern Hemisphere from this island; all four records are regarded as doubtful. Almost half of its species are known from the Antarctic, the remainder reach their southernmost limit within the sub-Antarctic region. About 47% of the South Georgian marine algae are known from sub-Antarctic islands at similar or more northerly latitudes and mainland South America (see Tables 1, 2). The remainder are confined to more southerly latitudes with a few reaching their northernmost limit at South Georgia (e.g. *Desmarestia antarctica*).

Table 1 An analysis of the marine benthic algae of South Georgia.

	Distribution					
	A	s-A	SG only	SG+TF only	NH	SG type loc.
Acrosiphonia pacifica	+	+	–	–	+	–
Adenocystis utricularis	+	+	–	–	–	–
Ahnfeltia plicata	+	+	–	–	+	–
Anisocladella serratodentata	–	+	–	+	–	+
Antithamnion ptilota	–	+	–	–	–	–
Ascoseira mirabilis	+	+	–	–	–	+
Ballia callitricha	+	+	–	–	–	–
Bostrychia vaga	–	+	–	–	–	–
Caepidium antarcticum	–	+	–	–	–	–
?*Calliblepharis ciliata*	–	+	–	–	+	–
Callithamnion montagnei	–	+	–	–	–	–
?*Callonema olivaceum*	–	+	–	–	+	–
?*Callophyllis cristata*	–	+	–	–	+	–
Callophyllis linguata	–	+	–	+	–	+
Callophyllis variegata	+	+	–	–	+	–
Ceramium diaphanum	–	+	–	–	+	–
Ceramium involutum	+	+	–	–	–	–
Ceramium rubrum	–	+	–	–	+	–
?*Choreocolax rhodymeniae*	–	+	–	+	–	+
Cladodonta lyallii	–	+	–	–	–	–
Cladophora incompta	–	+	–	–	–	–
Cladothele decaisnei	–	+	–	–	–	–
Clathromorphum obtectulum	–	+	–	–	–	–
Colacodasya inconspicua	–	+	–	–	+	–
Corycus lanceolatus	–	+	–	–	–	–
Curdiea recovitzae	+	+	–	–	–	–
Delesseria salicifolia	–	+	–	–	–	+
Delisea pulchra	+	+	–	–	–	–
Desmarestia antarctica	+	+	–	–	–	–
Desmarestia ligulata	–	+	–	–	+	–
Desmarestia menziesii	+	+	–	–	–	–
Desmarestia pteridoides	–	+	–	+	–	+
Desmarestia willii	+	+	–	–	–	–
Durvillaea antarctica	+	+	–	–	–	–
Ectocarpus constanciae	–	+	–	–	–	–
Ectocarpus exiguus	–	+	–	+	–	–
Ectocarpus siliculosus	–	+	–	–	+	–
Elachista meridionalis	–	+	–	+	+	–
Enteromorpha bulbosa	+	+	–	–	–	–
Enteromorpha gunniana	+	+	–	–	–	–
Entonema subcorticale	–	+	+	–	–	+
Entonema tenuissimum	–	+	–	–	+	–
Falklandiella harveyi	–	+	–	–	–	–
Geminocarpus austrogeorgiae	+	+	–	–	–	+
Geminocarpus geminatus	+	+	–	–	–	+
Georgiella confluens	+	+	–	–	+	–
Halopteris funicularis	–	+	–	–	–	–
Halopteris obovata	–	+	–	–	–	–
Heterosiphonia berkeleyi	+	+	–	–	–	–
Himantothallus grandifolius	+	+	–	–	–	–
Hydrolithon discoideum	–	+	–	–	–	–
?*Hymenocladiopsis crustigena*	+	+	–	–	–	–
Iridaea cordata (form)	+	+	–	–	–	–
Iridaea obovata	+	+	–	–	+	–
Lessonia fuscescens	–	+	–	–	–	–
Macrocystis pyrifera	–	+	–	–	+	–
Melastictis desmarestiae	–	+	+	–	–	+
Mesophyllum schmitzii	+	+	–	–	–	–
Microrhinus carnosus	–	+	–	+	–	+
?*Myriogramme livida*	–	+	–	–	–	–
Myriogramme smithii	+	+	–	–	–	–
Myrionema densum	–	+	–	–	–	–
Myrionema incommodum	+	+	–	–	–	+
Myrionema inconspicuum	–	+	–	+	–	+

Table 1 *cont.*

	Distribution					
	A	s-A	SG only	SG+TF only	NH	SG type loc.
Myrionema macrocarpum	–	+	–	–	–	–
Myrionema paradoxum	–	+	–	+	–	+
Nereoginkgo adiantifolia	+	+	–	–	–	–
Neuroglossum ligulatum	–	+	–	+	–	+
Nothogenia fastigiata	–	+	–	–	–	–
Palmaria decipiens	+	+	–	–	–	+
Palmaria georgica	+	+	–	–	–	+
Pantoneura plocamioides	+	+	–	–	–	+
Petalonia fascia	–	+	–	–	+	–
Petroderma maculiforme	+	+	–	–	+	–
Phaearthron austrogeorgica	–	+	–	+	–	+
Phycodrys austrogeorgica	–	+	–	+	–	+
Phycodrys quercifolia	+	+	–	–	–	–
Phyllophora antarctica	+	+	–	–	–	–
Phyllophora appendiculata	+	+	–	–	–	+
Picconiella plumosa	+	+	–	–	–	–
Pilayella littoralis	+	+	–	–	+	–
?*Plectoderma minus*	–	+	+	–	–	+
Plocamium cartilagineum	+	+	–	–	+	–
Plocamium hookeri	+	+	–	–	–	–
Plocamium secundatum	+	+	–	–	–	–
Polycoryne radiata	–	+	–	–	–	+
Polysiphonia anisogona	–	+	–	–	–	–
Porphyra endiviifolium	+	+	–	–	–	–
Porphyra umbilicalis	+	+	–	–	+	–
?*Prasiola crispa* (subsp. *antarctica*)	+	+	–	–	+	–
Prasiola filiformis (var. *minuta*)	–	+	–	–	–	–
Pseudolaingia larsenii	–	+	–	–	–	+
Pterothamnion simile	+	+	–	–	–	–
Sarcodia montagneana	–	+	–	–	–	+
Schizoseris condensata	–	+	–	–	–	+
Schizoseris dichotoma	–	+	–	–	–	–
Scytosiphon lomentaria	–	+	–	–	+	–
Scytothamnus fasciculatus	+	+	–	–	–	–
Stegastrum porphyrae	–	+	+	–	–	+
Synarthrophyton patena	+	+	–	–	–	–
Syringoderma australe	+	+	–	–	–	+
Ulva lactuca (var. *macrogyna*)	–	+	–	–	+	–
Utriculidium durvillaei	+	+	–	–	–	–

Key to abbreviations: A, Antarctic (latitudes <55° S); s-A, sub-Antarctic; SG, South Georgia; TF, Tierra del Fuego; NH, Northern Hemisphere.

A recent ordination analysis of the algal floras of the Southern Oceans by John et al. (1994) supports the findings of Lawson (1988: fig. 7) and Ricker (1987) who contend that the sub-Antarctic region represents a single circumpolar province. They observed no sharp discontinuity between the algal floras of the Antarctic and sub-Antarctic despite the principal surface water currents running counter to one another in the two regions. The close similarity between different sub-Antarctic islands is remarkable considering the remoteness and often vast distances separating many of them. It is speculated that much of the sub-Antarctic flora results from the long distance dispersal by the West Wind Drift of plants originating on South American shores.

In conclusion, further investigations are required to determine just how typical are the distribution patterns of algae in Husvik Harbour compared to other South Georgian shores. Advances in our knowledge of the seaweeds of South Georgia and the Southern Ocean in general continue to be hampered by lack of material (especially collected by SCUBA diving), paucity of taxonomic research on new or historically-important collections, absence of seasonal observation on shore algae and few experimental studies designed to provide information on dynamics including plant-animal interactions.

Table 2 Summary of an analysis of the marine benthic algae of South Georgia.

	Distribution					
	A	s-A	SG only	SG+TF only	NH	SG type loc.
Chlorophyta	4	5	1	0	4	1
Phaeophyta	14	21	2	6	7	13
Rhodophyta	29	28	1	6	11	18
TOTAL	47	54	4	12	22	32

Key to abbreviations: A, Antarctic (latitudes <55° S); s-A, sub-Antarctic region; SG, South Georgia; TF, Tierra del Fuego; NH, Northern Hemisphere.

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